Review

Scientia Marina 84(4)
December 2020, 463-475, Barcelona (Spain)
ISSN-L: 0214-8358
https://doi.org/10.3989/scimar.05091.24A

The benthos: the ocean's last boundary?*

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*Manuscript written on the occasion of Margalef Year (2019), commemorating the centenary of the birth of Ramon Margalef

Abstract: Benthic communities depend on receiving much of their food from the water column. While sinking, particles are transformed in a discontinuous process and are temporally retained in transitional physical structures, which act as boundaries and contribute to their further transformation. Motile organisms are well-acquainted with boundaries. The number, width and placement of boundaries are related to the degree of particle degradation or transformation. Progressively deepening within each boundary, particles are degraded according to their residence time in the discontinuity and the activity of the organisms temporarily inhabiting that boundary. Finally, particles reach the seafloor and represent the main food source for benthic organisms; the quality and quantity of this food have a strong impact on the development of benthic communities. However, benthic communities not only play the role of a sink of matter: they act as an active boundary comparable to other oceanic boundaries, in accordance with the boundary concept proposed by the ecologist Ramon Margalef.

Keywords: ocean boundaries; benthos; benthic-pelagic and pelagic-benthic coupling; Ramon Margalef.

El bentos: ¿la última frontera del océano?

Resumen: Gran parte del alimento de las comunidades bentónicas depende de lo que reciben de la columna de agua. Mientras las partículas se hunden, se transforman en un proceso discontinuo y se retienen temporalmente en estructuras físicas de transición, que actúan como fronteras y contribuyen a su posterior transformación. La movilidad de los organismos está relacionada con estas fronteras. el grado de degradación o transformación de las partículas está relacionado con el número, la amplitud y la ubicación de las fronteras. De manera progresiva y conforme van hundiéndose en la columna de agua, las partículas se degradan según el tiempo de residencia en la discontinuidad (frontera) y la actividad de los organismos que habitan temporalmente en la frontera. Por último, las partículas llegan al fondo marino y representan la principal fuente de alimento para los organismos bentónicos; la calidad y cantidad de este alimento ejercen un fuerte impacto en el desarrollo de las comunidades bentónicas. Sin embargo, las comunidades bentónicas no solo desempeñan el papel de sumidero de materia orgánica: actúan como una frontera activa -comparable a otras fronteras (discontinuidades) a lo largo de la columna de agua-, en el marco del concepto de frontera propuesto por el ecólogo Ramon Margalef.

Palabras clave: fronteras del océano; bentos; acoplamiento bento-pelágico y pelágico-béntico; Ramon Margalef.

Citation/Como citar este artículo: Gili J.-M., Vendrell-Simón B., Arntz W., Sabater F., Ros J. 2020. The benthos: the ocean's last boundary? Sci. Mar. 84(4): 463-475. https://doi.org/10.3989/scimar.05091.24A

Editor: D. Vaqué.

Received: June 2, 2020. **Accepted:** November 19, 2020. **Published:** November 26, 2020.

INTRODUCTION

The legacy of important scientists in ecology has not always been recognized by younger generations. Lesser-known contributions by a renowned ecologist may be overshadowed by their better-known ones and thus remain understudied and often unexplored. We find examples of this in many of the ideas proposed by Ramon Margalef, which are overshadowed by his renowned work related to phytoplankton ecology (Prat 2015, Prat et al. 2015). Particularly in the context of marine sciences, deserving greater attention are his innovative ideas on the role of boundaries as structures that could help to better understand the functioning of marine systems, as they intervene in the exchange of matter and energy between subsystems or bodies of water, accelerating or slowing down the exchange processes. The ideas proposed by Margalef (Margalef 1968, 1974, 1991, 1997) can help innovate ways of interpreting ocean structures and processes. The present paper is a modest contribution to Margalef's legacy, and it seeks to capture the same honesty and open-mindedness that characterized his teaching.

The benthos has traditionally been considered by many scientists as a sink of pelagic production (Turley 2000, Levin and Gooday 2003, Schewe and Soltwedel 2003). However, benthic communities not only play the role of a sink, as the whole benthic assemblage operates as a very active boundary between the seafloor and water (or air in exposed littoral zones) (Arntz et al. 1999). Due to friction between the seafloor and water, the currents near the bottom slow down, and consequently so does the transport of particles. This mechanism enhances the concentration of organisms approaching the bottom to feed (Berasategui et al. 2006, Gili et al. 2006). Particularly relevant in this process is the role of sessile animals, which filter and retain seston particles. Transforming them in a way similar to how zooplankton does in the water column, sessile benthic organisms contribute with their metabolic activity to the microbial loop near the bottom, releasing nutrients which may be used by microbial communities (Lovvorn et al. 2005). The combination of physical forces, such as sedimentation processes and near-bottom currents, with organism activity makes benthic communities an active living boundary between water column communities and sediments. The benthos acts as an interface, a biotic layer between the water and the substrate. This concept of an active boundary is in accordance with the boundary theory proposed by Margalef. The active benthic layer can be compared with other boundaries such as thermoclines, the interface between continental and coastal waters, the sea ice-water environment, etc. According to Margalef (Margalef 1974), benthic communities are a system that interacts with two closely related systems: water columns and substrates. Benthic communities transmit tension between these systems, incorporating exosomatic energy in such a way that the more organized system (the benthic community) takes in information (in the form of food, for example) from the less complex one (the water column) (Margalef 1968). Although the approach used here is based more on systems dominated by macrofauna that contribute to greater ecosystem complexity, the dominance of zooplankton in the water column must also be taken into account, as it contributes to a higher level of complexity in comparison with phytoplankton and microplankton water column communities. Comparisons made only on a macrofaunal level fail to shed light on key aspects: for example, on a microbial level, do benthic communities emerge as more complex, rather than more organized, than those thriving in the water column? As in other ocean boundaries, production is intensified near the bottom mainly due to increased interaction between elements of the water columns and the substrates involved. Finally, benthic communities could also be considered as ergoclines, in which physical and biological processes interact energetically and the transfer of matter occurs at different spatial and temporal scales, as it does in water column boundaries.

OCEAN BOUNDARIES

Most water mass boundaries described in oceanography refer to transitional physical structures, such as thermoclines, haloclines, Ekman layers, marine fronts and nepheloid layers. These ergocline regions have often been defined as areas of sharp gradients where vertical friction effects are important in terms of ecological flows. Such structures slow down the sinking or horizontal transport of suspended particles or planktonic organisms. It has long been recognized that these structures are places of strong biotic and abiotic interactions (Fagan et al. 2003), where suspended organic matter is temporarily retained and transformed by organisms (Turley 2000, Stemmann et al. 2004). The degree of degradation or transformation of the particles depends on the time they reside in the interface or boundary zone, as occurs in thermoclines or haloclines (Wotton 1994). Many authors generalize this idea, considering these boundaries as interface regions where the rate or magnitude of ecological flows (nutrients, organisms, matter, energy or information) changes abruptly relative to those of the surrounding water masses (Sheridan et al. 2002, Margalef 2001).

Other well-known ocean boundaries include the interface between surface waters and the atmosphere (where neuston and pleuston flourish) and the interface between the water column and the bottom sediment, where benthic organisms play a major role in the exchange of matter and energy (Meysman et al. 2006, Witte et al. 2003). Margalef (1974, 1991) considered these types of boundaries as places of direct ecological flows between two subsystems, one turbulent and one stable, where a high shear stress (or an analogous tension function) is generated. The exchange surface between subsystems is linear, enhancing a more direct interconnectivity. This type of boundary, described by van Leeuwen (1966) as *limes convergens*, is characterized by asymmetric exchanges. For instance, Margalef (1974) sees marine fronts as ergoclines separating water masses that are complementary in nutrient content and flow oppositely, thus maintaining the discontinuity, where biological production is enhanced. Most of

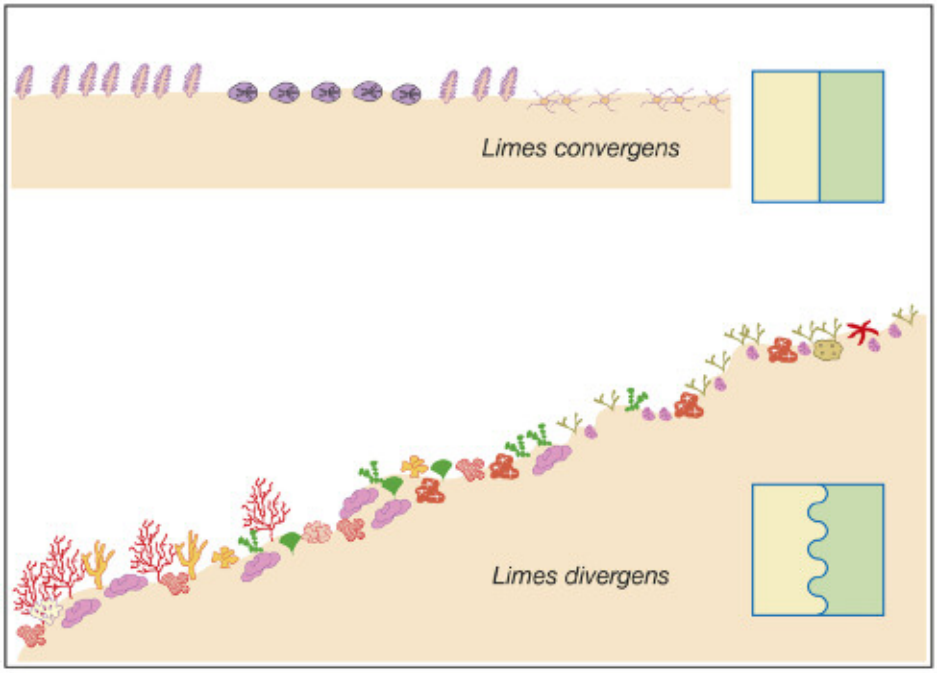

Fig. 1. – Different benthic profiles with linear, contrasting limits and low fractal limits (*limes convergens*) or sinuous, diffuse limits with a high fractal index (*limes divergens*). Redrawn from van Leeuwen (1966).

these boundaries are asymmetric, with more turbulent water on one side and more stratified water on the other. Productivity is higher on the turbulent side, whereas biomass accumulation is greater on the stratified one. Some examples have been studied in different benthic communities in which the epibenthic layer shows the highest production and the biomass accumulates in the form of sessile and long-lived organisms (Zabala and Ballesteros 1989, Brey and Gerdes 1998, Nilsen et al. 2006).

THE MARGALEFIAN CONCEPT OF THE BOUNDARY

Margalef (1968, 1974) accepted the division of boundaries proposed by van Leeuwen into two main types: *limes convergens* and *limes divergens*. *Limes convergens* are boundaries of rather linear surfaces and a low fractal index, whereas *limes divergens* are boundaries with irregular, sinuous surfaces and a high fractal index. Margalef considered that every ecosystem could be arbitrarily divided into contiguous subsystems or patches delimitated by boundaries, where asymmetries between subsystems may occur (Fig. 1).

One can assume that in *limes divergens* there is no preference in the transport or direction of trophic organization, and that in *limes convergens* adjacent parts are related in a trophic cycle, allowing for the distinction between different directions in transport. Diversity gradients are interesting if related to other differences, such as the contact between two subsystems differing in maturity and productivity. If the boundary is permeable, the less mature system may export a part of its excess production to the other one. Subsystems on either side of a boundary may differ in their state of maturity (as shown, e.g. by their biomass/production ratios). If they are markedly different, the more mature side will energetically exploit the less mature one, causing a greater asymmetry between the two sides. Interactions also entail motility and turbulence.

Components of ecosystems which seem more conservative can be dominant because they have structures enabling them to control exosomatic energy (benthic "forests", microbial mats, coral reefs) and maintain high diversity, indicating that exploiters diversify more than the exploited. Because of their slower turnover, organisms in these ecosystems increase their control in recirculating chemical components. Thus, internalization of information takes place: for example, construction of skeletal material, which involves a greater control of biochemical fluxes.

Ecologists usually make a distinction between plankton and benthos as if they were separate systems. Margalef proposed to consider them in a more systemic and complementary way. In line with his thinking, a much higher proportion of primary producers is found in surface plankton than in the benthos, where secondary producers and decomposers usually dominate. The two subsystems are complementary to each other. Production/respiration or production/biomass is greater in surface plankton, whose maintenance implies a net transport of labile organic matter from the plankton to the benthos. It has been said that benthos exploits plankton (Margalef 1974), but perhaps it is more accurate to say that benthos depends on plankton, as its major source of matter and energy comes from the planktonic system (Graf 1992). Furthermore, in turbulent waters, benthic primary producers are more efficient than plankton at supplying food to sessile animals or incorporating carbon. Benthic primary producers in turbulent waters incorporate more carbon than phytoplankton (Charpy-Roubau Sournia 1990). In the

layer near the bottom, benthos and plankton are part of the same boundary, as an important part of the benthic production is also exported to the planktonic system in a variety of compounds, particles and organisms (Koski et al. 2005). Even these organisms subsequently become plankton consumers (Boero et al. 1996).

Traditionally, ocean boundaries have been widely considered essential for biotic communities because they play functional roles in planktonic ecosystem dynamics, becoming transitory sinks for drifting organic and inorganic particles, delimiting planktonic populations and communities (Magnusson et al. 1981), and enhancing biodiversity (MacIntyre et al. 1995). For example, they control the flux of materials, reducing transport velocity, creating nutriclines and thus allowing microorganisms to accumulate and benefit from these organic and inorganic enrichments (Abell et al. 2000). These boundaries along the water column, such as thermoclines or haloclines, should be considered from an even more dynamic point of view as transition zones in the vertical flow of particles. In the sense proposed by Margalef (1997), unequal interactions occur in the physical-biological coupling processes that act across them. However, obvious inequalities do not always occur if the interactions between organisms are smooth, the sinking rate of particles is high and the residence time in the physical discontinuity is short (Hodges and Rudnick 2004).

Likewise, some relatively high nitrite concentrations in the water column may derive from bacterial denitrifies concentrated in certain ocean boundaries. The major sites of water column denitrification described in the ocean are the oxygen minimum zones, such as the one in the eastern South Pacific (Arntz et al. 2006). The importance of high productivity near boundaries in terms of cycling and transport of nutrients has been widely documented (McPhee-Shaw 2006). Therefore, there is strong evidence that physical, chemical and biological processes occurring at the ocean boundaries are crucial determinants of the fluxes of energy and matter throughout the ocean water column.

Many planktonic organisms are adapted to these regions. Zooplankton communities are well-acquainted with these boundaries and gather there to feed (Berasategui et al. 2006). However, the presence of zooplankton in such structures is not permanent because they avoid their predators, allowing for only the incomplete consumption of particles, though they also contribute to organic matter concentration and further sinking of the seston with their excretion and faeces. The foraging behaviour of many species of fish near water mass boundaries has also been described by different authors. For instance, the filter-feeding basking shark (*Cetorhinus maximus*) spends long periods foraging on high densities of zooplankton assemblages along thermal fronts (Sims and Quayle 1998). Margalef (1974) supports this idea of animals taking advantage of the opportunities that each subsystem offers, whether the organisms are adapted to living in the boundary or move from one side to the other. In the latter case, he proposes that animals that spend different activity periods in each of the subsystems should exhibit a different behaviour within each of them.

THE OCEAN AS A PUFF PASTRY

Envisioning the ocean as a "puff pastry", an analogy used frequently by Margalef, helps to understand it as a whole formed by subsystems limited by a series of boundaries. Longhurst (1985) interprets this idea as a multi-layer system, in which the different layers perpetuate physical, chemical and biological variables. The analogy of the ocean puff pastry includes both horizontal and vertical boundaries, such as pycnoclines found in the water column and marine fronts in areas near the continental margins, respectively.

Focusing on horizontal ergoclines and vertical transport of organic matter and particles, the ocean can be seen as an assemblage of convergent boundaries through which sinking matter undergoes different transformations until it reaches the benthos (Fig. 2). Among these transformations are microbial processing of organic matter (Bidle and Azam 1999, Bhaskar and Bhosle 2005), chemical breakdown (Sheridan et al. 2002, MacIntyre et al. 1995), foraging (Stemmann et al. 2004, MacIntyre et al. 1995, Gooday 2002), and aggregation or fragmentation (Stemmann et al. 2004, Alldredge 1979), which transform the sinking material and turn it into more refractory matter as it follows its path towards the seafloor. Qualitatively, settling material suffers an impoverishment as it travels from surface to bottom (Levin and Gooday 2003, Schewe and Soltwedel 2003). Transformations and reworking of organic matter also depend on the sedimentation rate of the particles and the number and types of boundaries they pass, which are in turn related to the depth of the water column and to the corresponding ecosystem. Long sinking paths with many horizontal boundaries will probably enable a greater transformation and reuse of the material than shorter sinking paths with fewer boundaries to go through, such as those occurring on the continental shelves (e.g. Schewe and Soltwedel 2003, Olli et al. 2002).

The type of benthic community which will develop depends, among other things, on the quality of the material reaching the seafloor (Levin and Gooday 2003, Van der Loeff et al. 2002). The more refractory the matter, with consequently less "available information", the more poorly it will be reused to construct a complex community (Fig. 3). An example of a long sinking path and of an increasing refractory proportion of matter reaching the seafloor is provided by Del Giorgio and Duarte (2002), particularly in open waters. Examples of short sinking paths are those on Antarctic continental shelves, where rich benthic communities of high density and high biomass develop (Gili et al. 2001). Although Antarctic continental shelves are deeper than those at other latitudes, the falling of particles, especially of phytoplankton from the surface after thawing, is very fast (Isla et al. 2006). Because the water temperature is between 0 and less than –1°C all year round, organic matter decomposes much more slowly than in tropical systems and maintains its nutritional potential for months (Gili et al. 2001). A similar example is given by Fukuchi et al. (1993) in the Bering Sea. These

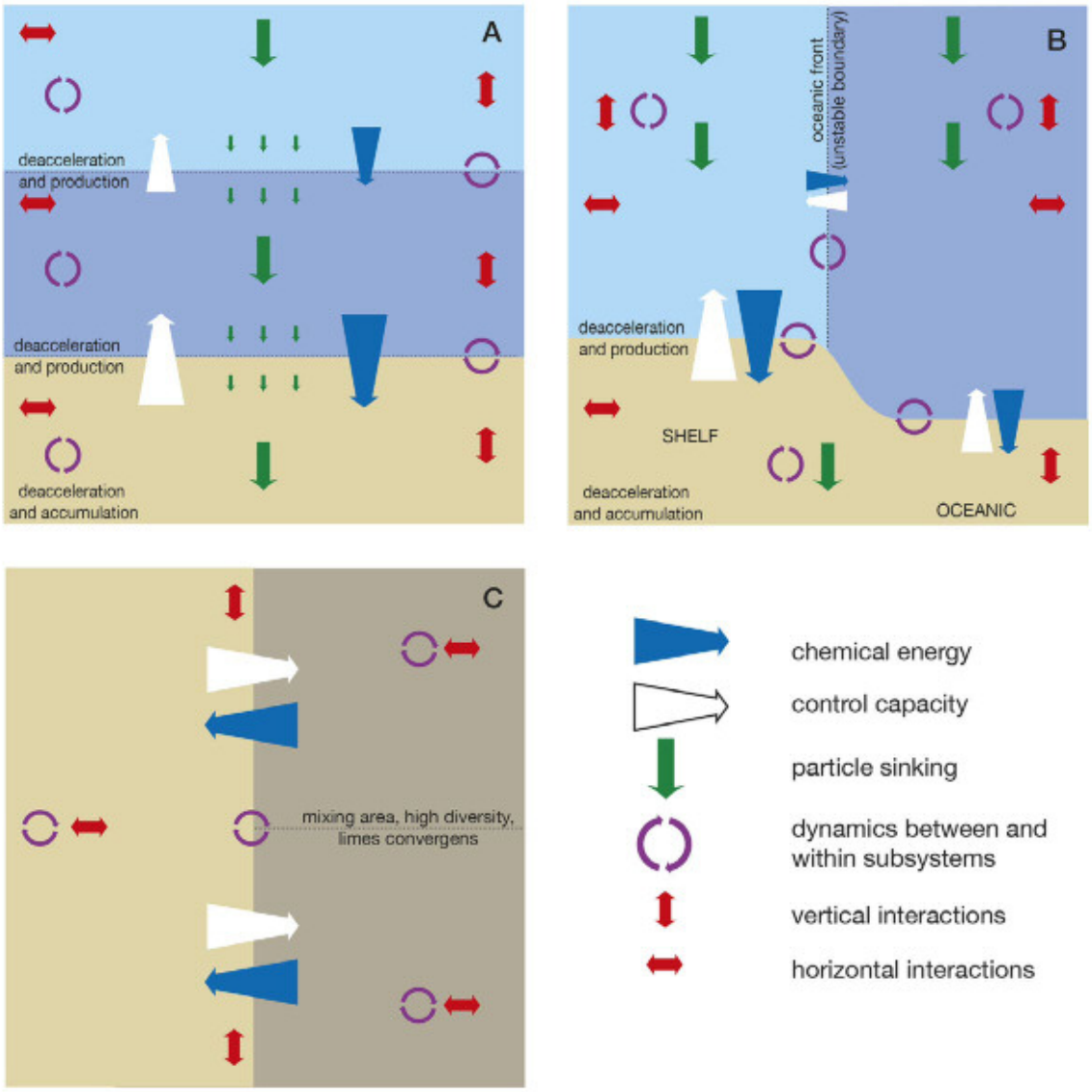

Fig. 2. – Schematic representation of interaction processes along asymmetric boundaries (reworked from Margalef 1974). The more organized subsystem receives energy from the less organized one and influences its future development. Boundaries of this type can only be stable when they are concentric (A). An intersection of boundaries is unstable (B) unless they are symmetric and passive (C), as is the case of two adjacent but different benthic communities in the same stage of maturity. Pelagic-benthic energy coupling is strong in mixed areas such as those associated with pelagic fronts (B), where an increase in organic matter loading may increase subsurface dwelling and organic matter processing by benthic biomass. On continental shelves, due to their shallowness, the interactions between subsystems from the surface to the seafloor seem to be greater than in oceanic areas, where particles must go through more boundaries and thus lose energy in each transfer (B). The return of the benthos is thus expected to be greater in shelf areas. Within boundaries, deceleration of particles occurs, giving rise to production events. If the benthos is considered as a boundary, deceleration would involve an accumulation of particles, which would in turn involve a production event and thus a return of organic and inorganic matter from the benthos to the water column.

examples support the hypothesis made by Grebmeier and McRoy (1989), which proposes that benthic communities reflect processes occurring in the overlying water. For this reason, the seabed and its associated benthic community have been traditionally considered the ultimate oceanic carbon or organic matter sink (Schewe and Soltwedel 2003, Buesseler et al. 2005, Parrish et al. 2005).

Margalef (1974) said that ecologists usually make distinctions between plankton and the benthos, as if their general organization would show marked differences, but he insisted on the idea that these differences may be studied just as an extrapolation of what is seen in different plankton patches of different maturity, emphasizing the complementarity of the two subsystems. In this context, the benthos and its activity should be considered an important transitional zone and part of the water-sediment interface that regulates the flux of materials and biogeochemical processes.

VERTICAL BOUNDARIES

In addition to the passive vertical transport of particles, there are other, non-constant but significant connection mechanisms between different water layers through discontinuities. The continental shelf break concentrates a series of processes and phenomena that occur along both the continental shelf and the slope. Sedimentary

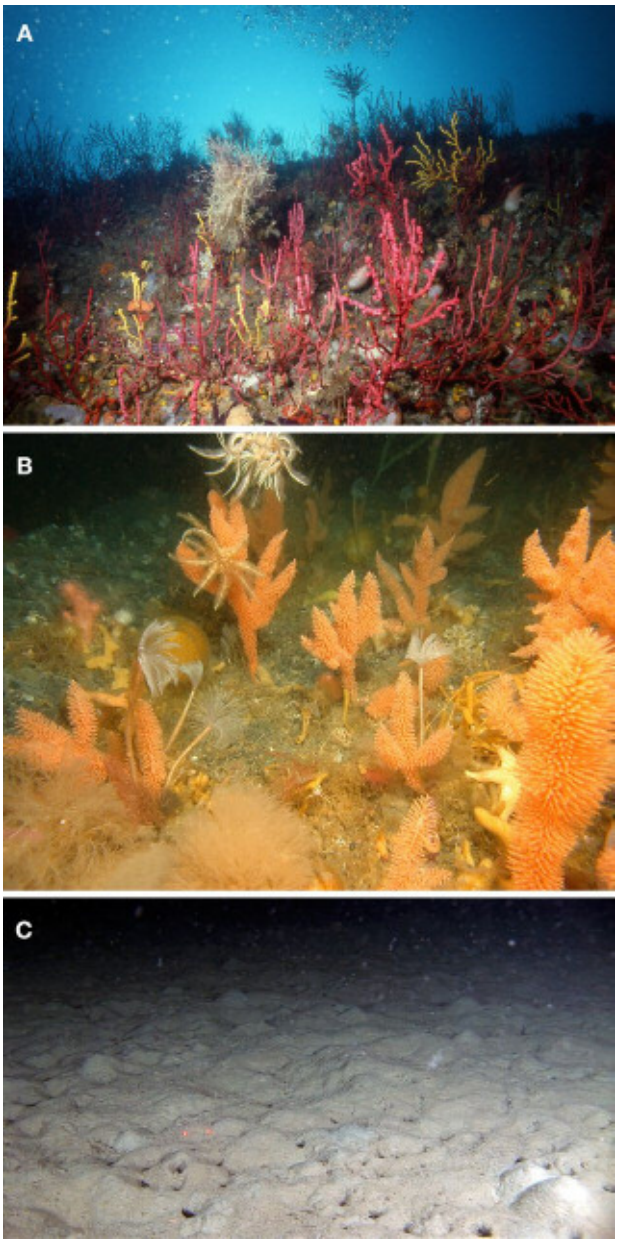

Fig. 3. – Benthic communities inhabiting (A) shallow coastal areas (Mediterranean), (B) continental shelves (Antarctic) and (C) the deep-ocean Mediterranean (Mediterranean). The type and complexity of the benthos found depends on the quantity and quality of energy reaching its habitat. Types A and B are typical of areas where distance from surface to bottom is shallower with fewer boundaries to go through. Type C represents a typical oceanic seafloor, where the materials coming from the water column above have long been reworked and contain less energy. (Pictures by A, J. Gili, ICM-CSIC; B, Julian Gutt AWI-Bremerhaven; C, Jürgen Schauer JAGO-GEOMAR-Kiel).

processes associated with continental run-off, together with coastal current regimes, suddenly change when the steepness of the shelf becomes strongly pronounced. At this point, hydrodynamic processes accelerate particle transport, generate upwelling and downwelling and increase turbulence, generally in association with hydrographic fronts (Huthnance 1995).

Processes linking the physics and the ecology of the shelf edge are wind-driven upwelling, the upwelling and downwelling (including cascades of shelf seawater and its constituents) driven by the bottom Ekman layer along slope flows and the development of semi-permanent shelf-slope hydrographic fronts (McGillicuddy 2016). The density fronts at the shelf break contribute to the formation of zooplankton concentrations, attributable both to the passive transport of organisms and to the active mechanism of spawning by adults in the most productive areas (Sabatés and Masó 1990). These processes of the shelf also contribute strongly to organic material export from neritic waters to open oceans and support important stocks of planktivorous fish (McIntyre 2010). The main geomorphologic structures, such as submarine canyons, contribute to the transfer of energy at different velocities from the shelf to the deep-sea through the vertical boundary between them (Puig et al. 2014). All these environmental and geomorphological features generate special habitat conditions on the seafloor that differ from those in other coastal and deep-sea marine areas. These particular habitats have led to the development of unique benthic communities in all oceans (Levin and Dayton 2009). The high biomass and biodiversity of benthic communities at the shelf break indicate strong pelagic-benthic coupling near the front, which may suggest a marked boundary area with a mixed water column. These are consistent with the hypotheses that pelagic-benthic energy coupling is stronger in mixed areas than in more stratified ones and that increased organic matter load may increase subsurface dwelling and matter processing by the benthic community (Josefson and Conley 1997).

THE BENTHOS AS A SINK?

Considering the water column in general, the benthos had always been regarded as a sink where the remains of water column production end (Bonsdorff and Blomqvist 1993). A sink is understood as the possible final destiny of the matter and energy from the pelagos. However, in areas where benthic communities are abundant, it has been shown that the organisms inhabiting the seafloor have a major impact on the ecosystem in which they dwell. They capture large quantities of particles and may directly regulate primary production and indirectly regulate secondary production, particularly in coastal and shallow food chains (Gili and Coma 1998). Moreover, benthic organisms create a set of bioengineering structures and processes that generate dynamic and complex habitat-mediated interaction webs, affecting the trophic web and meshed with it in the trophic web on the seafloor (Reise 2002). As an example, the benthos is an extremely active part of littoral systems, receiving the rain of food particles which settle and actively exploiting the production in the water column brought to them by current flows. However, vertical fluxes do not always supply sufficient food to benthic animals in shelf zones in the area directly below the pelagic region where the maximum biological production occurs. In these areas, bottom and tidal currents can compensate for the lack of vertical flow because horizontal advection together with resuspension of material from the bottom can result in higher amounts

of benthos-derived material in places relatively close to the substratum (Johnson 1988). The combination of tidal water and reduced salinities in shallow zones may create water column stratification and near-bottom currents of great importance for the particle supply and grazing impact exerted by benthic organisms (Larsena and Riisgård 1996). The interaction between organisms and seston is enhanced by turbulent mixing due to wind, wave and current action, hence increasing the coupling of benthic communities to pelagic biomass (Wildish and Kristmanson 1997). For seston to be continuously available to suspension feeders, the water layer surrounding them must be continuously renewed (Eckman and Duggins 1993). Therefore, the coupling between hydrodynamic forces and particle fluxes (from "marine snow" to organisms) drives all biological processes in seafloor communities.

The relationship between benthic activity and production and the pulses of vertical fluxes as events of external food supply is a well-known phenomenon in both shallow and deep areas (Fig. 4). For example, the spring development also triggering reproduction of the benthic community in temperate seas is strongly influenced by vertical flux events of the preceding summer and autumn (Caron et al. 2004, Thiem et al. 2006); this also occurs in high latitude environments (Isla et al. 2006). In temperate spring systems, all phytoplankton blooms which sedimented were consumed by the benthos within 5-6 weeks (Graf and Rosenberg 1997). In deep-sea food-limited environments, the extent of enrichment of organic carbon (by the increasing flux settling onto the seabed) alters the structure of benthic communities, as an increasing flux may increase their diversity and biomass (Witte 1996, Harrold et al. 1998). A similar seasonal pulse of detrital material to bathyal and abyssal depths was shown at temperate latitudes (Billet et al. 1983). This material seems to be directly derived from surface primary production and seems to have rapidly sunk towards the deep-sea benthos (Henson et al. 2006). Moreover, Van der Loeff et al. (2002) described that benthic suspension feeders can contribute to the deposition of particles advected from productive ice-free regions in the Arctic.

In many geographic areas, the result of water column production reaches the bottom in better nutritive conditions for the benthos than was previously thought (Witte 1996). Seston and marine snow sink towards the bottom as intact particles, in different states of degradation depending on the distance from the photic zone (Wotton 1994), or packed in faecal pellets, and contribute greatly to the enrichment of the benthic boundary layer. The quality of the food that reaches the seafloor may also be increased by the reduced pelagic bacterial activity in low temperature waters (Vogel 1994). On the other hand, both the activity of suspension feeders and resuspension events seem to enhance bacterial production near the bottom, which, in turn, provides a supplementary particulate carbon source for benthic requirements (Gooday 2002, Van der Loeff et al. 2002). In conclusion, the development of benthic communities is a combination of three main factors: hydrodynamic regimes, quantity and quality of food supply and the possibility of benthic organisms, at the population and community levels, to interact with environmental conditions and modify water flows and near-bottom trophic webs, particularly the microbial loop. These three factors can be applied to every marine community.

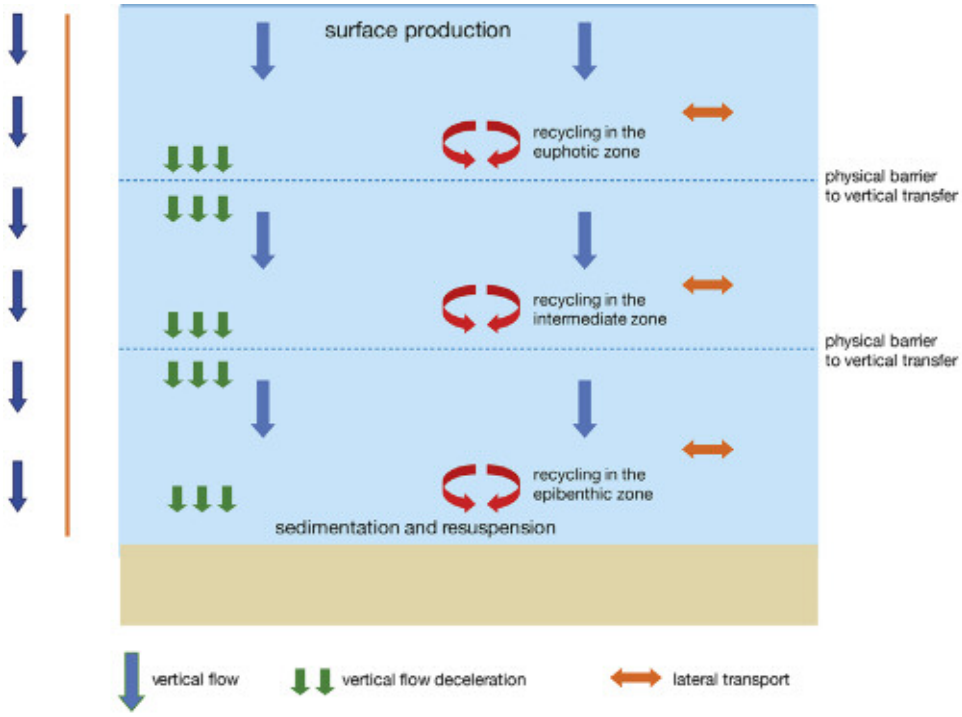

Fig. 4. – Schematic representation of the relationship between benthic communities and vertical fluxes along water column discontinuities.

Benthic sessile organisms develop dense populations organized into three-dimensional communities in which structural complexity is mainly regulated by flow speed (Vogel 1994). Consequently, communities—especially those dominated by suspension feeders—make up a highly active boundary system somehow different to the discontinuities or ecotones between communities in the water column (Margalef 1997). The system is highly structured and quite efficient in exploiting the plankton, a less complex system because ecological succession develops faster in planktonic communities, reaching less biomass per unit space. Benthic communities, especially those of high diversity, reach a greater maturity through ecological succession and, with it, greater structural complexity and biomass (Margalef 1991). At different spatial levels, the difference between the two systems is that benthos is patchier than plankton and benthic biomass does not often correspond to the biological production processes of the water column just above the seafloor (Sherrell et al. 1998, Ichino et al. 2015).

The benthic boundary layer in waters close to the seafloor may be seen as a distinct environment, as it contains a higher abundance of particles and microorganisms (Ritzrau et al. 1997). Hydrodynamic processes near the seafloor, such as resuspension, sort the organic from the inorganic fraction within the particulate matter (Thomsen 1999). The organic fraction has low settling velocities which enhance its residence time in the water column and aggregate formation before settling or biodeposition (Thomsen et al. 1998). Associated with this organic particle maintenance in the water column, there is high microbial biomass and activity (Ritzrau and Thomsen 1997), leading to the transformation and remineralization of particulate organic matter. In addition, with the increase of bacterial abundance, the overall effect of resuspension and near-bottom water transport is the supply of a significantly large amount of bacterial carbon to the total particulate organic carbon pool of suspended particles (Ritzrau and Graf 1992). Benthic organisms also play a clear complementary role in the biological processes occurring at the benthic boundary layer, as they filter particles or release organic and inorganic nutrients generated by metabolic processes. The physicochemical interactions between animals and seston (Vogel 1994) enhance particle residence time in near-bottom water masses and the formation of aggregates that provide food availability to benthic communities, but also nutrient release. Van der Loeff et al. (2002) proposed that where a benthic nepheloid layer is well-developed, the bottom fauna should be characterized by suspension feeders, which can best benefit from it.

Suspension feeders, e.g. sponges and corals, modify seston composition through several mechanisms used in prey capture, such as breaking up aggregates into small particles, decelerating them so that they become available to other organisms, and introducing other particles and substances generated by their feeding activity (e.g. Witte et al. 1997). Other species aggregate small particles in the form of faecal pellets, which are an important food source for deposit feeders (e.g. Amouroux et al. 1990), or supply organic matter which could be useful for near-bottom microbial production. These processes enhance particle flux from the water column to the seabed through biodeposition and provide food for other benthic fauna. All these processes related to the maintenance of food quality in sediments and its continuous resuspension are key phenomena for understanding changes in benthic biomass and production.

The activity of benthic macroorganisms such as sessile invertebrates influences the nutrient concentration near the seafloor, as has been observed in coral reefs (Richter et al. 2001), the high Antarctic (Orejas et al. 2001), and the North Atlantic (Davoult et al. 1990), where most exchanges of carbon and nitrogen between the pelagic and benthic compartments are due to the activity of dense populations of suspension feeders. Such high values of organic nutrients, if compared with their concentration in the water column, are an evidence of the role of benthic communities in organic matter remineralization processes (Grebmeier and Barry 1991). However, bacterial activity in benthic habitats must not be neglected, as Witte et al. (2003) showed in a study conducted off the west coast of Norway, in which bacteria outcompeted macrofauna in their capacity to process fresh particulate organic matter coming from the water column above. The increase in bacterial biomass and activity and the release of organic and inorganic nutrients in the benthic boundary layer, in addition to which several authors have considered resuspension as a biomass input term to the pelagic system (Wainwright 1990, Tenore et al. 2006), is thus a major characteristic of this frontal system. For instance, Fanning et al. (1982) indicated that resuspension of as little as 1 mm^3 of shelf sediment could intermittently increase overlying productivity by as much as 100% to 200% in the Gulf of Mexico, thus accelerating nutrient recycling on the continental shelf and slope. Regeneration of micronutrients on the seafloor is also likely to be facilitated by the frequent occurrence of a poorly stratified water column, allowing for an enhanced vertical mixing (Barry et al. 1988).

Many exceptions to conceptual models are found in the ocean. In the present proposal of the benthos as "the last frontier", an exception of sorts is found in the Antarctic. On the underside of the sea ice, there are primary producers, grazers, fish, even suspension feeders (Daly et al. 2013). All ecological processes occur in a layer less than one metre thick during the winter, which, after disintegrating during the summer, builds up again at the beginning of the following winter. The underside of the ice is probably a simplified specular version of the bottom communities but, in any case, a simplified version of sea life living on the seafloor anywhere, including bathyal habitats, which are very poor in macrofaunal abundance. Abundant neuston and pleuston (e.g., in the Sargasso Sea) fulfil another of these specular versions of bottom benthos.

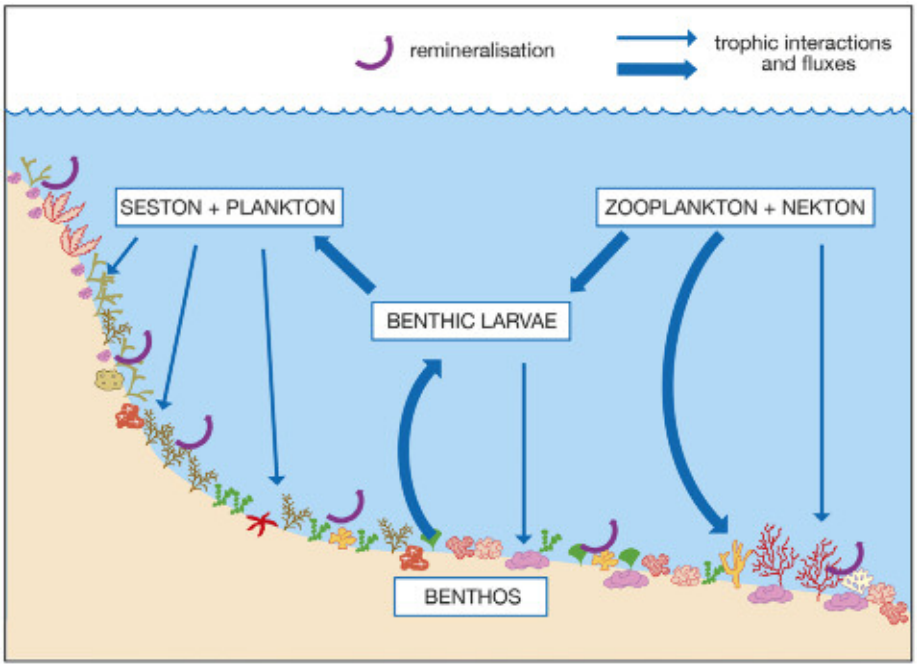

Fig. 5. – Trophic relationships between the benthic system and the water column system. From a classical point of view, the benthos exploits plankton by feeding on seston and plankton organisms that passively or actively reach the seafloor and by sending larvae to feed directly on plankton. A less considered relationship is the predation of zooplankton and nekton organisms on benthic larvae or directly on benthic animals (both sessile and motile). Another relationship of interest is the contribution of benthic activity to organic matter remineralization, enhancing the nutrient "way back" (purple arrows).

THE WAY BACK

Vertical migration of zooplankton is a well-documented phenomenon that is mainly driven by animals foraging in food-rich surface waters at night and migrating from tens to hundreds of metres below to escape predation or reduce metabolism at lower temperatures (Richter et al. 2001). However, recent evidence supports the hypothesis that these migrations also have a different important trophic component because zooplankton exploits particle and seston concentrations near the bottom (Gili et al. 2006, Clarke and Tyler 2008). One of the main seston components present throughout the water column is marine snow, found in great abundance in the benthic boundary layer (Caron et al. 2004). These aggregates play a significant role in epibenthic zooplankton activity, which also contributes to the remineralization of organic matter near the bottom (Smetacek 1984). If it is accepted that the benthos can contribute to the formation and transformation of aggregates, zooplankton feeding near the bottom serves as a way of later transporting materials upwards in the water column.

Other examples of upward coupling (benthic-pelagic vs. pelagic-benthic, Smetacek 1984) include pelagic and nektonic predators exploiting benthic prey. Excursions to the seabed and the trophic activity of nektonic organisms on benthic communities are not constant but have a relevant impact on pelagic-benthic coupling processes. For example, a review of data from several seas and from the Southern Ocean (Wainwright 1990, Arntz et al. 1994, Tenore et al. 2006, Smith et al. 2006) shows that many fish, seabirds and mammals obtain their food sources from benthic organisms or feed on them. In some species of whales, such as the grey whale (Fanning et al. 1982, Schonberg et al. 2014), the prey-switching and prey-habitat selection behaviour between planktonic and benthic prey is driven by a decline in the abundance of or changes in the size of water column prey. Furthermore, Gutt and Siegel (1994) describe an upward trophic link mediated by krill that feed on the seafloor and are then consumed by pelagic fish or mammals, and Gili et al. (2006) report a similar situation in which salps swim to the bottom to feed on marine snow and are predated by sessile alcyonaceans. The present paper suggests that exploitation of benthic prey by pelagic predators may be especially important on the Antarctic shelf during ice-covered winter months, when water column production is very low (Smetacek 1984). Though many species that migrate to near-bottom layers prefer less predictable prey (plankton) to more predictable prey (benthos), the seafloor is a key food source during certain periods and a relevant "way back" for biological production.

One of the best-known "ways back" is larval release from benthic organisms (Fig. 5). Larvae sent temporally to the pelagic subsystem exploit plankton, and few of them return to the benthos because most of them are predated in the water column (Valiela 1995). In addition to exerting a trophic pressure on the plankton, the migration towards the water column of the larval phases of benthic organisms is one of the most important ways back to the pelagic system. The larvae are a food source for many pelagic species. Larval survival and dispersal are key to understanding the importance of the benthic-pelagic coupling processes near the seafloor (Arntz and Gili 2001). All

these data allow us to reconsider the hypothesis of the "superprudent" predator (Slobodkin 1961, Margalef 1974), the hypothetical organism that returns organic matter from ocean depths to surface waters.

THE IMPACT OF BENTHIC SUSPENSION FEEDERS ON NEAR-BOTTOM PLANKTONIC BACTERIAL COMMUNITIES

Benthic communities living on Antarctic shelves are often dominated by suspension feeders, among which sponges can be very abundant. Experiments were carried out on several Antarctic cruises on board RV *Polarstern*, during which specimens of the demosponge *Stylocordyla chupachups* were incubated in order to determine their effect on the surrounding water (Vendrell et al. 2005). In these experiments, it was observed that sponges do indeed feed on bacteria, as bacterial abundance decreased with incubation time (Fig. 6a), but they seem to enhance both the inorganic nutrient enrichment (Fig. 6B) of the water and bacterial production (Fig. 6A). The results from a spring cruise are shown, indicating the impact of the sponges on the bacterial communities near the bottom. This effect occurs widely in these rich communities of benthic suspension feeders, contributing to the return of energy and matter to the water column as a less organized and less mature system.

The capacity of bacteria processing fresh organic matter has been stated by Witte et al. (2003) and Lovvorn et al. (2005), who proposed that matter reworked by bacteria is made available to the macrobenthos. Schewe and Soltwedel (2003) expect to find a higher bacterial abundance in bottom areas where a sedimentation event has occurred. Thus, benthic activity should be further affected by sinking matter pulses, and the ability of benthic communities to exploit the planktonic system closely links the two systems. The degree of this coupling is related both to the organic matter that the benthos obtains from the water column and to the benthic-derived material which returns to the plankton in the form of nutrients or organic particles. Thus, a mussel bed community may exploit a planktonic system with a food web that contains few secondary consumers (e.g. in estuarine systems). By comparison, sublittoral communities that exploit littoral planktonic systems with more diverse consumers are at the opposite end of the spectrum. In such systems, the presence of a thermocline increases the structure and production of the communities in the water column, and the subsequent breakdown of the thermocline furnishes the benthos with a broad spectrum of particles and organisms (Bonsdorff and Blomqvist 1993). In the open ocean, energy transfer flows vertically, gradually descending through the water column with a considerable loss of surface production by the time it reaches the bottom (Smetacek 1984). In contrast, in shallow ecosystems benthic organisms have more immediate access to fresh planktonic production due to the proximity of the photic layer to the bottom, and also due to mixing by tidal or wind-generated currents.

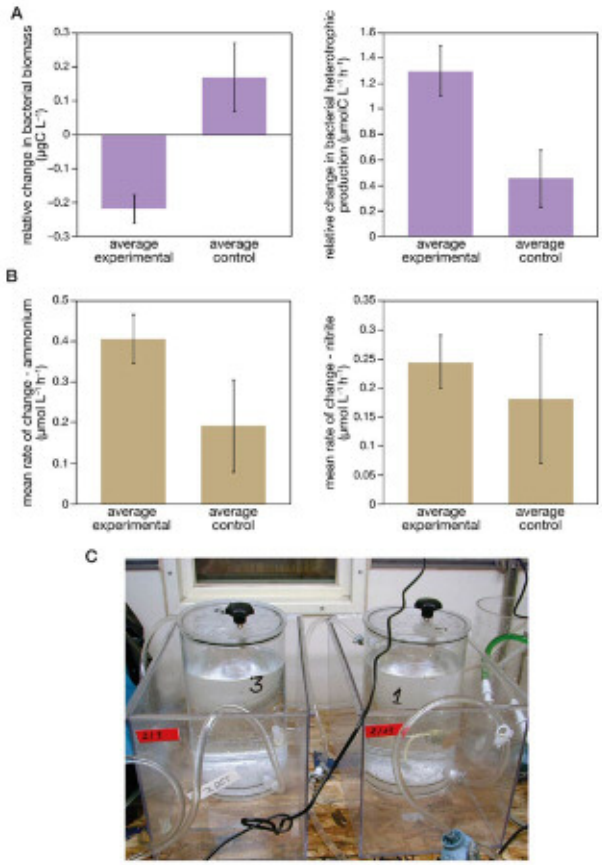

Fig. 6. – Experiments with the demosponge *Stylocordyla chupachups* (C) showing that sponges feed on bacteria, as bacterial abundance decreases (A left) and bacteria production increases (A right), but also enhance inorganic nutrient enrichment of water with both ammonium (B left) and nitrite (B right), increasing incubation time.

A better-known aspect of benthic-pelagic coupling is related to grazing by benthic invertebrates on small plankton in the water column. Planktonic cells less than 5 µm in size, known as nano- and picoplankton, are the main contributors to marine productivity and biomass (Valiela 1995), and their interactions constitute the marine microbial food web. This trophic web has been extensively studied in the water column and has received much attention from planktologists in the past few decades. Also, as mentioned above, a well-known example of benthic-pelagic coupling is that found in benthic organisms that spend part of their life cycles in the water column, in the form of meroplanktonic larvae. The degree to which the benthos can thus contribute to pelagic life differs among benthic size fractions and is most important in tropical and temperate seas (Valiela 1995). Most outstanding is the effect of grazing by benthic invertebrates on water column communities in shallow, near-shore ecosystems, both near the bottom and indeed in the water column when larvae are released; hence, their impact on the microbial food web is greater (Gili and Coma 1998). Considering the benthos of polar areas, the contribution to the pelagos is higher in the Antarctic than in the Arctic because the diversity and biomass of Antarctic communities are an order of magnitude greater than those of the Arctic (Arntz et al. 1994).

Finally, we conclude that there is significant evidence of upward benthic-pelagic coupling in shelf ecosystems involving two processes: diffusion of dissolved nutrients and changes in the microbial community via near-bottom water upwelling; and temporal visiting and predation of plankton swarms. Active transport, both vertical and horizontal, together with continuous organic matter transformation just above the bottom, corroborates the role of the benthos as an active boundary in the context of Margalefian thought. The importance of the "benthic boundary" depends on the amount of external energy that it processes, being much greater in shelf communities than in deep communities.

ACKNOWLEDGEMENTS

Professor Margalef passed away in the summer of 2004. His legacy and his teaching will be remembered by many for a long time to come. With this paper, the authors wish to thank him not only for the vast knowledge he shared but also for his honesty and the tremendous enthusiasm that he always showed when communicating with his students. We also wish to thank all colleagues in the Department of Evolutionary Biology, Ecology and Environmental Sciences of the University of Barcelona and the Institut de Ciències del Mar - CSIC of Barcelona for the informal conversations held over the past few years, which have helped develop the ideas conveyed in the present work. Part of this paper was presented as a lecture for students at the 1st Symposium *Omnis cellula* at the Faculty of Biology of the University of Barcelona in 2004. Part of it was also presented at the scientific meeting, "*La unidad en la diversidad: un congreso de ecología tras el legado de Ramon Margalef*" (Barcelona, 2008). We want to especially thank Jordi Corbera for the illustrations and diagrams accompanying the text and Kimberly Katte for the English revision. This work was supported by the LIFE+INDEMARES (LIFE07 NAT/E/000732) project. The authors are especially grateful for the contributions made by two anonymous reviewers who helped to improve this work.

REFERENCES

Abell J., Emerson S., Renaud P. 2000. Distributions of TOP, TON and TOC in the North Pacific subtropical gyre: Implications for nutrient supply in the surface ocean and remineralization in the upper thermocline. J. Mar. Res. 58: 203-222. https://doi.org/10.1357/002224000321511142

Alldredge A.L. 1979. The chemical composition of macroscopic aggregates in two neritic seas. Limnol. Oceanogr. 24: 855-866. https://doi.org/10.4319/lo.1979.24.5.0855

Amouroux J.M., Amouroux J., Bastide J., et al. 1990. Interrelations in a microcosm with a suspension-feeder and a deposit-feeder. I. Experimental study. Oceanol. Acta 13: 61-68.

Arntz W.E., Gili J.M. 2001. A case for tolerance in marine ecology: let us not put out the baby with the bathwater. Sci. Mar. 65 (Suppl. 2): 283-299. https://doi.org/10.3989/scimar.2001.65s2283

Arntz W.E., Brey T., Gallardo V.A. 1994. Antarctic zoobenthos. Oceanogr. Mar. Biol. Ann. Rev. 32: 241-304.

Arntz W.E., Gili J.M., Reise K. 1999. Unjustifiably ignored: reflections on the role of benthos in marine ecosystems. In: Gray J.S., Ambrose W. Jr., et al. (eds) Biogeochemical Cycling and Sediment Ecology, Kluwer Academic Publishers, Dordrecht, pp. 105-124. https://doi.org/10.1007/978-94-011-4649-4_5

Arntz W.E., Gallardo V.A., Gutiérrez D., et al. 2006. El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems. Adv. Geosci. 6: 243-265. https://doi.org/10.5194/adgeo-6-243-2006

Barry J.P. 1988. Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. Polar Biol. 8: 377-391. https://doi.org/10.1007/BF00442029

Berasategui A.D., Menu Marque S., Gómez-Erache M., et al. 2006. Copepod assemblages in a highly complex hydrographic region. Est. Coast. Shelf Sci. 66: 483-492. https://doi.org/10.1016/j.ecss.2005.09.014

Bhaskar P.V., Bhosle N.B. 2005. Microbial extracellular polymeric substances in marine biogeochemical processes. Curr. Sci. 88: 45-53.

Bidle K., Azam F. 1999. Accelerated dissolution of diatom silica by marine bacterial assemblages. Nature 397: 508-512. https://doi.org/10.1038/17351

Billet D.S.M., Lampitt R.S., Rice A.L., et al. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302: 520-522. https://doi.org/10.1038/302520a0

Boero F., Belmonte G., Fanelli G., et al. 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? Trends Ecol. Evol. 11: 177-180. https://doi.org/10.1016/0169-5347(96)20007-2

Bonsdorff E., Blomqvist E.M. 1993. Biotic coupling on shallow water soft bottoms - Examples from the Northern Baltic Sea. Oceanogr. Mar. Biol. Ann. Rev. 31: 153-176.

Brey T., Gerdes D. 1998. High Antarctic macrobenthic community production. J. Exp. Mar. Biol. Ecol. 231: 191-200. https://doi.org/10.1016/S0022-0981(98)00060-4

Buesseler K.O., Andrews J.E., Pike S.M., et al. 2005. Particle export during the Southern Ocean Iron Experiment (SOFeX). Limnol. Oceanogr. 50: 311-327. https://doi.org/10.4319/lo.2005.50.1.0311

Caron G., Michel C., Gosselin M. 2004. Seasonal contributions of phytoplankton and faecal pellets to the organic carbon sinking flux in the North Water (northern Baffin Bay). Mar. Ecol. Prog. Ser. 283: 1-13. https://doi.org/10.3354/meps283001

Charpy-Roubaud C., Sournia A. 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. Mar. Micro. Food Webs 4: 31-57.

Clarke A., Tyler P.A. 2008. Adult Antarctic krill feeding at abyssal depths. Curr. Biol. 18: 282-285. https://doi.org/10.1016/j.cub.2008.01.059

Daly M., Rack F., Zook R. 2013. *Edwardsiella andrillae*, a new species of sea anemone from Antarctic Ice. PloS ONE 8: e83476. https://doi.org/10.1371/journal.pone.0083476

Davoult D., Gounin F., Richard A. 1990. Dynamique et reproduction de la population d'*Ophiothrix fragilis* (Abildgaard) du détroit du Pas-de Calais (Manche orientale). J. Exp. Mar. Biol. Ecol. 138: 201-216. https://doi.org/10.1016/0022-0981(90)90167-B

Del Giorgio P.A., Duarte C.M. 2002. Respiration in the open ocean. Nature 420: 379-384. https://doi.org/10.1038/nature01165

Eckman J.E., Duggins D.O. 1993. Effects of flow speed on growth of benthic suspension feeders. Biol. Bull. 185: 28-41. https://doi.org/10.2307/1542128

Fagan W., Fortin M-J., Soykan C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. BioScience 53: 730-738. https://doi.org/10.1641/0006-3568(2003)053[0730:IEDADM]2.0.CO;2

Fanning K.A., Carter K.L., Betzer P.R. 1982. Sediment resuspension by coastal waters: a potential mechanism for nutrient re-cycling on the ocean's margins. Deep-Sea Res. Part A 29: 953-965. https://doi.org/10.1016/0198-0149(82)90020-6

Fukuchi M., Sasaki H., Hattori H., et al. 1993. Temporal variability of particulate flux in the northern Bering Sea. Cont. Shelf Res. 13: 693-704. https://doi.org/10.1016/0278-4343(93)90100-C

Gili J.M., Coma R. 1998. Benthic suspensión feeders: their para-

mount role in littoral marine food webs. Trends Ecol. Evol. 13: 316-321. https://doi.org/10.1016/S0169-5347(98)01365-2
Gili J.M., Coma R., Orejas C., et al. 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world? Polar Biol. 24: 473-485. https://doi.org/10.1007/s003000100257
Gili J.M., Rossi S., Pagès F., et al. 2006. A new trophic link between the pelagic and benthic systems on the Antarctic shelf. Mar. Ecol. Prog. Ser. 322: 43-49. https://doi.org/10.3354/meps322043
Gooday A.J. 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: A review. J. Oceanogr. 58: 305-332. https://doi.org/10.1023/A:1015865826379
Graf G. 1992. Benthic-pelagic coupling: a benthic view. Oceanogr. Mar. Biol. Annu. Rev. 30: 149-190.
Graf G., Rosenberg R. 1997. Bioresuspension and biodeposition: a review. J. Mar. Syst. 11: 269-278. https://doi.org/10.1016/S0924-7963(96)00126-1
Grebmeier J.M., Barry J.P. 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. J. Mar. Syst. 2: 495-518. https://doi.org/10.1016/0924-7963(91)90049-Z
Grebmeier J.M., McRoy C.P. 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas -III. Benthic food supply and carbon cycling. Mar. Ecol. Prog. Ser. 53: 253-268. https://doi.org/10.3354/meps051253
Gutt J., Siegel V. 1994. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). Deep Sea Res. I 41: 169-178. https://doi.org/10.1016/0967-0637(94)90031-0
Harrold C., Light K., Lisin S. 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forest. Limnol. Oceanogr. 43: 669-678. https://doi.org/10.4319/lo.1998.43.4.0669
Henson S.A., Sanders R., Holeton C., et al. 2006. Timing of nutrient depletion, diatom dominance and a lower-boundary estimate of export production for Irminger Basin, North Atlantic. Mar. Ecol. Prog. Ser. 313: 73-84. https://doi.org/10.3354/meps313073
Hodges B.A., Rudnick D.L. 2004. Simple models of steady deep maxima in chlorophyll and biomass. Deep-Sea Res. Part I 51: 999-1015. https://doi.org/10.1016/j.dsr.2004.02.009
Huthnance J.M. 1995. Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. Progr. Oceanogr. 35: 353-431. https://doi.org/10.1016/0079-6611(95)80003-C
Ichino M.C., Clark M.R., Drazen J.C., et al. 2015. The distribution of benthic biomass in hadal trenches: a modelling approach to investigate the effect of vertical and lateral organic matter transport to the seafloor. Deep-Sea Res. Part I 100: 21-33. https://doi.org/10.1016/j.dsr.2015.01.010
Isla E., Gerdes D., Palanques A., et al. 2006. Particle flux and tides near the continental ice edge on the eastern Weddell Sea shelf. Deep-Sea Res. Part II 53: 866-874. https://doi.org/10.1016/j.dsr2.2006.02.010
Johnson A.S. 1988. Hydrodynamic study of the functional morphology of the benthic suspension feeder *Phoronopsis viridis* (Phoronida). Mar. Biol. 100: 117-126. https://doi.org/10.1007/BF00392961
Josefson A.B., Conley D.J. 1997. Benthic response to a pelagic front. Mar. Ecol. Prog. Ser. 147: 49-62. https://doi.org/10.3354/meps147049
Koski M., Kiorboe T., Takahashi K. 2005. Benthic life in the pelagic: Aggregate encounter and degradation rates by pelagic harpacticoid copepods. Limnol. Ocaenogr. 50: 1254-1263. https://doi.org/10.4319/lo.2005.50.4.1254
Larsena P.S., Riisgård H.U. 1996. Mixing generated by benthic filter-feeders: a diffusion model for near-bottom phytoplankton depletion. J. Sea Res. 37: 81-90. https://doi.org/10.1016/S1385-1101(97)00009-9
Levin L.A., Dayton P.V. 2009. Ecological theory and continental margins: where shallow meets deep. Trends Ecol. Evol. 24: 606-617. https://doi.org/10.1016/j.tree.2009.04.012
Levin L.A., Gooday A. 2003. The deep Atlantic Ocean. In: Tyler P.A., Ecosystems of the World, Vol. 28, Ecosystems of the deep oceans. Elsevier, Amsterdam, pp. 111-178.
Longhurst A.R. 1985. Relationship between diversity and the vertical structure of the upper ocean. Deep-Sea Res. Part A 32: 1535-1570. https://doi.org/10.1016/0198-0149(85)90102-5
Lovvorn J.R., Cooper L.W., Brooks M.L., et al. 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. Mar. Ecol. Prog. Ser. 291: 135-150. https://doi.org/10.3354/meps291135
MacIntyre S., Alldredge A.L., Gotschalk C.C. 1995. Accumulation of Marine Snow at Density Discontinuities in the Water Column. Limnol. Oceanogr. 40: 449-468. https://doi.org/10.4319/lo.1995.40.3.0449
Magnusson J.J., Harrington C.L., Stewart D.J., et al. 1981. Responses of macrofauna to short-term dynamics of a gulf stream front on the continental shelf. In: Richards F.A., Coastal Upwelling I, Coastal and Estuarine Sciences, American Geophysical Union, pp. 441-448.
Margalef R. 1968. Perspectives in Ecological Theory. The University of Chicago, Chicago.
Margalef R. 1974. Ecología. Ed. Omega, Barcelona.
Margalef R. 1991. Teoria de los Sistemas Ecológicos. Publicacions de la Universitat de Barcelona. Barcelona.
Margalef R. 1997. Our Biosphere. Excellence in Ecology. Ecology Institute. Oldendorf.
Margalef R. 2001. The top layers of water bodies, a most important although relatively neglected piece of the biosphere plumbing. In: Gili J.-M., Pretus J.M., Packard T.T. (eds) A Marine Science Odyssey into the 21st Century. Sci. Mar. 65 (Suppl. 2): 207-213. https://doi.org/10.3989/scimar.2001.65s2207
McGillicuddy Jr. D.J. 2016. Mechanisms of physical-biological-biogeochemical interaction at the oceanic mesoscale. Annu. Rev. Mar. Sci. 8: 125-159. https://doi.org/10.1146/annurev-marine-010814-015606
McPhee-Shaw E. 2006. Boundary-interior Exchange: Reviewing the idea that internal-wave mixing enhances lateral dispersal near continental margins. Deep-Sea Res. Part II 53: 42-59. https://doi.org/10.1016/j.dsr2.2005.10.018
Meysman F.J.R., Middelburg J.J., Heip C.H.R. 2006. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol. 21: 691-694. https://doi.org/10.1016/j.tree.2006.08.002
Nilsen M., Pedersen T., Nilssen E.M. 2006. Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. Mar. Ecol. Prog. Ser. 32: 67-77. https://doi.org/10.3354/meps321067
Olli K., Riser C.W., Wassmann P., et al. 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. J. Mar. Syst. 38: 189-204. https://doi.org/10.1016/S0924-7963(02)00177-X
Orejas C., Gili J.-M., López-González P.J., et al. 2001. Feeding strategies and diet composition of four species of Antarctic cnidarian species. Polar Biol. 24: 620-627. https://doi.org/10.1007/s003000100272
Parrish C.C., Thompson R.J., Deibel D. 2005. Lipid classes and fatty acids in plankton and settling matter during the spring bloom in a cold ocean coastal environment. Mar. Ecol. Prog. Ser. 286: 57-68. https://doi.org/10.3354/meps286057
Prat N. 2015. Ramon Margalef 1919-2004. Una obra ingente no totalmente bien reconocida. Ecosistemas 24: 97-103. https://doi.org/10.7818/ECOS.2015.24-1.17
Prat N., Ros J. D., Peters F. 2015. Biografía científica del profesor Ramon Margalef López. In: Prat N., Ros, J. D., Peters F. (eds) Ramon Margalef, ecólogo de la biosfera. Una biografía científica, Universitat de Barcelona, Fundació Agbar, pp. 19-99.
Puig P., Palanques A., Martín J. 2014. Contemporary sediment-transport processes in submarine canyons. Ann. Rev. Mar. Sci. 6: 53-77. https://doi.org/10.1146/annurev-marine-010213-135037
Reise K. 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48: 127-141. https://doi.org/10.1016/S1385-1101(02)00150-8
Richter C., Wunsch M., Rasheed M., et al. 2001. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413: 726-730. https://doi.org/10.1038/35099547
Ritzrau W., Graf G. 1992. Increase of microbial biomass in the ben-

thic turbidity zone of Kiel Bight after resuspension by a storm event. Limnol. Oceanogr. 37: 1081-1086. https://doi.org/10.4319/lo.1992.37.5.1081
Ritzrau W., Thomsen L. 1997. Spatial distribution of particle composition and microbial activity in the benthic boundary layer (BBL) of the Northeast Water Polynya. J. Mar Syst. 10: 415-428. https://doi.org/10.1016/S0924-7963(96)00073-5
Ritzrau W., Thomsen L., Lara R.J., et al. 1997. Enhanced microbial utilisation of dissolved aminoacids indicates rapid modification of organic matter in the benthic boundary layer. Mar. Ecol. Prog. Ser. 156: 43-50. https://doi.org/10.3354/meps156043
Sabatés A., Masó M. 1990. Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the western Mediterranean. Deep-Sea Res. Part A 37: 1085-1098. https://doi.org/10.1016/0198-0149(90)90052-W
Sheridan C.C., Lee C., Wakeham S.G., et al. 2002. Suspended particle organic composition and cycling in surface and midwaters of the ecuatorial Pacific Ocean. Deep-Sea Res. Part I 49: 1983-2008. https://doi.org/10.1016/S0967-0637(02)00118-8
Schewe I., Soltwedel T. 2003. Benthic response to ice-edge-induced particle flux in the Arctic Ocean. Polar Biol. 26: 610-620. https://doi.org/10.1007/s00300-003-0526-8
Schonberg S.V., Clarke J.T., Dunton K.H. 2014. Distribution, abundance, biomass and diversity of benthic infauna in the Northeast Chukchi Sea, Alaska: Relation to environmental variables and marine mammals. Deep Sea Research Part II 102: 144-163. https://doi.org/10.1016/j.dsr2.2013.11.004
Sheridan C.C., Lee C., Wakeham S.G., et al. 2002. Suspended particle organic composition and cycling in surface and midwaters of the equatorial Pacific Ocean. Deep-Sea Res. Part I 49: 1983-2008. https://doi.org/10.1016/S0967-0637(02)00118-8
Sherrell R.M., Field M.P., Gao Y. 1998. Temporal variability of suspended mass and composition in the Northeast Pacific water column: relationships to sinking flux and lateral advection. Deep-Sea Res. Part II 45: 733-761. https://doi.org/10.1016/S0967-0645(97)00100-8
Sims D.W., Quayle V.A. 1998. Selective foraging behaviour of basking sharks on zooplancton in a small-scale front. Nature 393: 460-464. https://doi.org/10.1038/30959
Slobodkin L.B. 1961. Growth and Regulation of animal Populations. Holt, Rinehart & Winston, New York.
Smetacek V. 1984. The supply of food to the benthos. In: Fasham M.J.R. (ed.) Flows of energy and materials in marine ecosystems. Theory and practice. Plenum Press, pp. 517-547. https://doi.org/10.1007/978-1-4757-0387-0_20
Smith C.R., Mincks S., DeMaster D.J. 2006. A synthesis of benthopelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change. Deep-Sea Res. Part II 53: 875-894. https://doi.org/10.1016/j.dsr2.2006.02.001
Springer A.M., McRoy C.P., Flint M.V. 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. Fish. Oceanogr., 5(3-4): 205-223. https://doi.org/10.1111/j.1365-2419.1996.tb00118.x
Stemmann L., Jackson G.A., Gorsky G. 2004. A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes - Part II: application to a three year survey in the NW Mediterranean Sea. Deep-Sea Res. Part I 51: 885-908. https://doi.org/10.1016/j.dsr.2004.03.002
Tenore K.R., Zajac R.N., Terwin J., et al. 2006. Characterizing the role benthos plays in large coastal seas and estuaries: A modular approach. J. Exp. Mar. Biol. Ecol. 330: 392-402. https://doi.org/10.1016/j.jembe.2005.12.042
Thiem Ø., Ravagnan E-. Fossa J.H., et al. 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. J. Mar. Syst. 60: 207-219. https://doi.org/10.1016/j.jmarsys.2005.12.004
Thomsen L. 1999. Processes in the benthic boundary layer at continental margins and their implication for benthic carbon cycle. J. Sea Res. 41: 73-86. https://doi.org/10.1016/S1385-1101(98)00039-2
Thomsen L., Van Weering C.E. Tj. 1998. Spatial and temporal variability of particulate matter in the benthic boundary layer at the N.W. European continental margin (Goban Spur). Progr. Oceanogr. 42: 61-76. https://doi.org/10.1016/S0079-6611(98)00028-7
Turley C. 2000. Bacteria in the cold deep-sea benthic boundary layer and sediment-water interface of the NE Atlantic. Microbiol. Ecol. 33: 89-99. https://doi.org/10.1111/j.1574-6941.2000.tb00731.x
Valiela I. 1995. Marine Ecological Processes. Springer-Verlag, New-York. https://doi.org/10.1007/978-1-4757-4125-4
Van der Loeff M.M.R., Meyer R., Rudels B., et al. 2002. Resuspension and particle transport in the benthic nepheloid layer in and near Fram Strait in relation to faunal abundance and ^{234}Th depletion. Deep-Sea Res. Part I 49: 1941-1958. https://doi.org/10.1016/S0967-0637(02)00113-9
Van Leeuwen C.G. 1966. A theoretical approach to pattern and process in vegetation. Wentia 15: 25-46. https://doi.org/10.1111/j.1438-8677.1966.tb00019.x
Vendrell B., Gili J.M., Gasol J.M., et al. 2005. How do benthic antarctic communities impact near-bottom water layer properties? ASLO Summer Meeting 2005, 18-24 Junio, Santiago de Compostela.
Vogel S. 1994. Life in moving fluids: The physical biology of flow. University Press Princeton.
Wainwright S.C. 1990. Sediment-to-water fluxes of particulate material and microbes by resuspension and their contribution to the planktonic food web. Mar. Ecol. Prog. Ser. 62: 271-281. https://doi.org/10.3354/meps062271
Wildish D., Kristmanson D. 1997. Benthic suspension feeders and flow. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511529894
Witte U. 1996. Seasonal reproduction in deep-sea sponges - triggered by vertical particle flux? Mar. Biol. 124: 571-581. https://doi.org/10.1007/BF00351038
Witte U., Brattegard T., Graf G., et al. 1997. Particle capture and deposition by deep-sea sponges from the Norwegian-Greenland Sea. Mar. Ecol. Prog. Ser. 154: 241-252. https://doi.org/10.3354/meps154241
Witte U., Aberle N., Sand M., et al. 2003. Rapid response of a deep-sea benthic community to POM enrichment: an in situ experimental study. Mar. Ecol. Prog. Ser. 251: 27-36. https://doi.org/10.3354/meps251027
Wotton R.S. 1994. Particulate and disolved organic matter as food. In: Wotton R.S. (eds), The biology of Particles in aquatic systems, Lewis Publishers, Boca Raton, pp. 235-288. https://doi.org/10.1201/9781003070146-10
Zabala M., Ballesteros E. 1989. Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. Sci. Mar. 53: 3-17.